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Microbial control of the dark end of the biological pump

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Abstract

A fraction of the carbon captured by phytoplankton in the sunlit surface ocean sinks to depth as dead organic matter and faecal material. The microbial breakdown of this material in the subsurface ocean generates carbon dioxide. Collectively, this microbially mediated flux of carbon from the atmosphere to the ocean interior is termed the biological pump. In recent decades it has become clear that the composition of the phytoplankton community in the surface ocean largely determines the quantity and quality of organic matter that sinks to depth. This settling organic matter, however, is not sufficient to meet the energy demands of microbes in the dark ocean. Two additional sources of organic matter have been identified: non-sinking organic particles of debated origin that escape capture by sediment traps and exhibit stable concentrations throughout the dark ocean, and microbes that convert inorganic carbon into organic matter. Whether these two sources can together account for the significant mismatch between organic matter consumption and supply in the dark ocean remains to be seen. It is clear, however, that the microbial community of the deep ocean works in a fundamentally different way from surface water communities.

In the sunlit surface waters of the ocean, phytoplankton convert carbon dioxide into particulate organic carbon. A significant fraction of this newly produced particulate organic carbon is remineralized—that is, respired back to carbon dioxide—in these surface waters. However, about 1 to 40% of the photosynthetically fixed carbon is exported into the dark realm of the ocean where it is remineralized at substantially slower rates than in surface waters[1]. The resultant increase in dissolved inorganic carbon concentrations towards the interior of the ocean, coined the biological pump, is regulated by food web processes such as grazing.

Non-living particles, termed ‘marine snow’[2-4], transport organic matter to depth in the ocean. These particles comprise decaying phytoplankton, faecal matter generated by zooplankton, the most abundant multicellular organisms in the oceanic water column, and aggregates of high-molecular-weight dissolved organic matter released by phytoplankton in the senescent stage of blooms, or as a result of an imbalance in nutrient supply ratios[5,6]. The aggregation of high-molecular-weight dissolved organic matter, largely in the form of

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polysaccharides, leads to the formation of non-sinking nano- and microgels, and ultimately to the formation of larger, sinking particles[7]. Bacteria can colonize these particles, potentially increasing their stability and specific density, and hence settling velocity, through the release of polymeric compounds such as polysaccharides[8-10].

The biological pump essentially constitutes the downward transport of this particulate organic carbon, and the enrichment of carbon dioxide in the deep sea that results from its remineralization (Fig. 1). The efficiency of the biological pump is expressed as the ratio of carbon exported from the surface layer of the ocean to the total amount of carbon produced by phytoplankton primary production[1]. The amount of particulate organic carbon exported from the surface is influenced by biological and physical processes. For instance, microbial degradation and zooplankton fragmentation, and the physical disaggregation of particles due to turbulence, decrease particle flux with depth.

It has been suggested[11] that particulate organic carbon flux towards the ocean's interior follows a simple power law rule of the form $F = F_{100} \times (z/100)^{-b}$, based on sediment trap data. The parameter F_{100} indicates the particulate organic carbon flux at 100 m depth, and z is the depth of the sediment trap. The unitless parameter b determines the transfer efficiency of the particles and, more generally, sets the depth of remineralization in the deep sea, that is, the depth at which the sinking organic carbon is converted back to carbon dioxide. Originally little spatial variability was assumed in open ocean particle fluxes to the deep. But initial findings from the Joint Global Ocean Flux Study — an international programme designed to quantify carbon sedimentation rates in different ocean basins — indicated that the exponent b varies by an order of magnitude over different trophic regions of the global ocean, due to variations in particulate organic carbon export estimates at 100 m depth[12]. Thus, knowledge of the magnitude of export at the base of the euphotic zone, the sunlit upper region of the ocean where net primary production by phytoplankton takes place, is key to estimates of particle flux attenuation. Estimates of the proportion of phytoplankton primary production exported out of the euphotic layer, however, vary by up to an order of magnitude depending on the hydrography of the water column, nutrient availability, the composition of the phytoplankton community, the amount of primary production, and the intensity of zooplankton grazing[13].

Variations in particle flux

Fundamental to the size and velocity of sinking particles is the composition of the particulate material produced in the surface ocean. Regions harbouring siliceous diatoms such as the temperate North Atlantic and the Southern Ocean are characterized by substantial and fast particle flux, owing to the aggregation of diatoms, or the rapid sinking of diatom-derived siliceous material in zooplankton faecal pellets[14]. In more nutrient-rich (eutrophic) regions such as the northern North Atlantic, zooplankton faecal pellets tend to contribute more to total particulate organic carbon flux in mesopelagic (200–1000 m depth) and bathypelagic (1000–4000 m depth) waters than in nutrient-poor regions[15]. However, during intense phytoplankton blooms, such as the North Atlantic spring bloom, a significant fraction of the phytoplankton escapes zooplankton grazing and sinks relatively rapidly into the mesopelagic layer[15].

Oligotrophic (that is, nutrient-poor) regions such as the subtropical and tropical open oceans are dominated by smaller phytoplankton than eutrophic regions. These waters are characterized by slowly sinking small particles, primarily transformed by heterotrophic bacteria (those bacteria that use organic compounds as a carbon and energy source) in the mesopelagic realm. As such, it has been assumed that the microbe-sized picophytoplankton, 0.2–2 μm in diameter, that characterize the vast oligotrophic areas of the ocean do not

contribute significantly to particulate organic carbon flux in the ocean. But aggregating picophytoplankton exhibit sinking speeds comparable to those of larger algae, and may contribute equally to surface carbon export considering their dominance in the extensive gyre systems[16] (Fig. 2).

A recent survey of the distribution of particles ranging between 250 μm and 1.5 mm in the Atlantic and Pacific Oceans using underwater video profilers points to a coupling between phytoplankton community structure in the euphotic zone, the size of the particles exported, and the extent of the attenuation of vertical particle flux towards the dark ocean[17,18] (Fig. 3). Phytoplankton composition explained about 70% of the variability in particle flux at 300 m depth in these waters. Two patterns emerged. In eutrophic regions, aggregates — dominated by microphytoplankton such as diatoms — exhibited a high mass flux, but a sharp reduction in flux between 100 and 300 m, resulting in a high *b* value. Zooplankton degradation contributed significantly to the rapid reduction in particle flux in mesopelagic waters in these regions. In oligotrophic regions, aggregates were dominated by picophytoplankton, and exhibited a lower mass flux but a higher transfer efficiency, and thus relatively low values of *b*. Owing to the slow sinking rates of these aggregates, bacterial remineralization was considered the main mechanism of particle degradation in these waters (Fig. 3).

A new conceptual framework of particle flux to the dark ocean was recently developed that better captures seasonal differences in particle flux at different oceanic sites, compared with common curve-fitting procedures, such as the approach described above[13]. This conceptual model uses three metrics to estimate changes in particulate organic carbon flux with depth: (1) net primary production in the euphotic layer; (2) the ratio of particulate organic carbon flux at the lower end of the euphotic layer (the euphotic layer depth) relative to net primary production in the euphotic layer; and (3) the ratio between particulate organic carbon flux 100 m below the euphotic layer depth to that in the euphotic layer depth (Fig. 4). The relationship between particulate organic carbon flux 100 m below the euphotic zone and net primary production in turn characterizes the strength and efficiency of the biological pump. According to this model, particulate organic carbon export out of the euphotic zone accounts for between 1 and 40% of the net primary production at different oceanic sites (Fig. 4). The North Atlantic represents an extremely strong and efficient biological pump in this model because about half of the net primary production is exported out of the euphotic zone; the transfer efficiency is close to 100%, resulting in the export of over 40% of the net primary production out of the euphotic zone (Fig. 4). This new model challenges the hypothesis that enhanced particle sinking rates in the ocean correlate with the calcium carbonate and organic carbon content of sinking particles[16]. It also indicates that seasonality, the composition of phytoplankton species, the fragmentation of particles by zooplankton, and the solubilization of particles by microbes, all determine the overall transfer efficiency of the biological pump and its regional variability.

Uncertainties remain regarding the magnitude and speed of particle flux into the dark ocean, and the degree to which this flux varies over space and time. The fate of the particulate organic carbon reaching the meso- and bathypelagic ocean is even more uncertain, although it is generally assumed that this sinking material ultimately provides the food for essentially all heterotrophic life in the deep sea. Heterotrophic microbes and zooplankton are the main groups of organisms responsible for the remineralization of particles at depth in the oceanic water column. Knowledge about their relative contributions to particle transformation in the meso- and bathypelagic realm is in its infancy[3,4].

Sinking versus buoyant particles

Particle fluxes in the deep ocean are mostly measured using surface-tethered and moored sediment traps[19,20]. However, substantial turbulence might impede the efficiency with which sinking particles are collected by these traps[21,22]. Such turbulence effects are greatly reduced by using neutrally buoyant free-floating sediment traps, but whether the use of such traps improves the reliability of particle capture remains inconclusive[23].

The importance of slow-sinking and buoyant particles in the biological pump has been largely ignored, probably because of the reliance on sediment traps for collecting particles. Recent developments in underwater camera systems have, however, revealed striking differences in the attenuation of submicrometre- to centimetre-sized particles with depth[24]. Average concentrations of submicrometre- to centimetre-sized particles of organic carbon of around 2 mmol C m^{-3} have been reported throughout the water column of the subtropical North Atlantic, with no discernable decrease with depth[25]. The concentration of these apparently buoyant detrital particles is around one to two orders of magnitude higher than that of sinking particles collected by sediment traps[25]. A tight correlation between the respiratory activity of microbes and suspended particulate organic carbon indicates that metabolic activity in the dark ocean is closely tied to the buoyant fraction of the particle pool[26]. Furthermore, oxygen deficits in distinct layers of the deep equatorial North Atlantic have been linked to an abundance of macroscopic particles greater than 500 μm in diameter[18], suggesting that large particles may also be buoyant, residing within these layers long enough to be broken down by microbes.

The origin of slow-sinking and buoyant particles — that is, those particles that are largely missed by sediment traps — remains unclear. One possibility is that they are simply remnants of fast-sinking particles fragmented by deep-water organisms. Fragmentation of marine snow in the surface ocean by shear stress due to swimming zooplankton may contribute to the buoyant particle pool[27], but evidence for a zooplankton-mediated fragmentation of the pool of large and fast-sinking particles in the dark ocean is missing. Furthermore, there seems to be limited exchange between fast-sinking and buoyant particles in the mesopelagic realm, where buoyant particles are either fresher than fast-sinking particles such as zooplankton faecal pellets, or at a similar stage of degradation[28-30].

The rather stable concentration of buoyant particles in the dark ocean is in striking contrast to the rapid attenuation of fast-sinking particles collected by deep sediment traps. Consequently, one might hypothesize that at least a fraction of the buoyant particles are produced autochthonously at depth, with the remainder derived from slow-sinking marine snow-type particles that are generated in surface waters and become buoyant following entry into denser waters. Assuming that bacteria and archaea serve as a source of suspended carbon in the dark ocean, bacterial and archaeal biomass would need to accumulate for roughly 5 years to reach the suspended particulate organic carbon stock of 2 mmol C m^{-3} observed in the North Atlantic. Evidence for a significant marine snow source comes from measurements of the radiocarbon delta ^{14}C content of suspended particulate organic carbon in the mesopelagic North Pacific and North Atlantic[31], which indicate that suspended non-living particles could originate from the surface ocean and have a turnover time of 8 to 10 years.

The fate of the buoyant particle pool is equally uncertain. Recent measurements conducted in the northern North Atlantic suggest a complete remineralization of buoyant particles[32]. But the rather steady concentration of buoyant particles in meso- and bathypelagic layers obtained by video imaging and *in situ* sampling apparently contradicts this conclusion[18,25],

and supports a longer turnover time, as indicated by carbon isotope ratios of suspended particulate organic carbon[31].

The concentration, origin and fate of buoyant particles in the dark ocean remains uncertain. Sediment-trap sampling is not the best approach for sampling deep-water particles. Selective sampling using remotely operated underwater vehicles or submarines is required to determine the chemical composition and natural isotopic signature of fast-sinking versus buoyant particles, and to refine our view of the origin and fate of these two types of dark ocean particle.

Microbial activity in the dark

Sinking particles serve as hotspots of microbial activity in the deep ocean[33,34]. The abundance of microbes in a given volume of particle is up to three orders of magnitude higher than the abundance of free-living microbes in the same volume of sea water[34]. Furthermore, cell-specific extracellular enzyme activity and biomass production of particle-associated microbes is generally higher than that of free-living microbes[26,35]. The vast majority of these rate measurements have been performed under surface pressure conditions. However, particles might undergo substantial changes in hydrostatic pressure as they sink through the water column.

Very few studies have considered the effects of a shift in hydrostatic pressure on the activity of particle-attached microbes. However, species-specific maxima in the growth rates of selected bacterial strains at specific pressure conditions have been reported[36]. And in a study of phytoplankton-derived particles and their associated microbial communities, extracellular enzyme activity was found to decline with increasing hydrostatic pressure, although the composition of the bacterial community seemed unaffected[37]. From the limited information currently available, no firm conclusions can be drawn about the extent to which hydrostatic pressure affects microbial community composition and activity as particles sink through the water column.

From a microbial point of view, living in the dark ocean represents a challenge. Free-living heterotrophic microbes are faced with an increasingly refractory dissolved organic matter pool available for metabolism[38]. In contrast, particle-attached microbes might have access to higher concentrations of organic substrate. Indeed, radiocarbon studies indicate that the particulate organic matter pool in the ocean’s interior is substantially younger, and consequently of higher nutritive value, than the dissolved organic matter pool[39,40]. Hence, the higher cell-specific activity reported for particle-associated microbes corresponds to the higher nutritive quality of particles compared with dissolved organic matter in the surrounding sea water.

Differences in the composition and concentration of organic matter in the particulate and dissolved phase may be reflected in the physiology and life strategy of particle-associated versus free-living microbes in the deep ocean. Indeed, particle-associated microbes are thought to be typical copiotrophic organisms, that is, adapted to variable substrate concentrations and capable of rapid growth under nutrient-rich conditions[41]. These copiotrophic microbes are thought to maintain a more diverse enzymatic machinery, and consequently harbour a larger genome, than their nutrient-impoverished counterparts[41].

Although the principal ecological strategies of particle-associated and free-living microbes have been described, there is only rudimentary knowledge about actual differences in the phylogenetic composition[42] and life strategy of free-living and attached microbes in the dark ocean, and their relative abundance. This uncertainty stems from an inability to sample deep-water particles selectively[43]. Genomic information, however, indicates that particle-

associated and free-living microbial communities are phylogenetically[44] and functionally different[45,46], and that particle-attached microbes may be common in the deep ocean**.** Deep-sea microbes overexpress, relative to the surface water microbial community, genes required for the synthesis of pili (polymeric structures used for bacterial attachment on particles), polysaccharides and antibiotics, all indicative of a predominately particle-attached lifestyle[47,48]. An example is the copiotrophic Gammaproteobacterium *Alteromonas macleodii*, occurring in two ecotypes, one surface and one deep-water[49]: the deep-water ecotype shows genetic adaptations to low temperatures, microaerobic conditions, particle attachment and the potential to degrade recalcitrant organic matter[49]. Furthermore, deep-water prokaryotes generally possess a larger genome than their surface-water counterparts, considered to be indicative of a more versatile, opportunistic life mode[41,45]. Taken together, the genomic information obtained so far suggests that deep-sea microbes are better adapted to a particle-attached lifestyle than their surface-water counterparts. Furthermore, bacteria inhabiting diffusion-limited, confined environments, such as particles, release their extracellular enzymes (typically bound to the cell surface in free-living bacteria) into the environment[50]. Almost all deep-water extracellular enzymatic activity (>90%) is found in the dissolved phase[51], further supporting the notion of a preferential particle-attached lifestyle of microbes in the deep ocean.

Collectively, there is mounting, albeit indirect, evidence that deep-sea microbial activity is concentrated on particles[26,43,47]. Sampling these deep-water particles, however, is difficult. Conventional sampling of deep waters using bottles mounted on a rosette sampler generates turbulence destructive to these often fragile aggregates. As a consequence, conventional sampling leads to the homogenization of what is probably a highly structured nutrient-rich microenvironment within the nutritive desert of ambient waters. Measuring microbial activity on intact deep-water particles remains a challenge, even more so under *in situ* pressure conditions.

Deep-water energy demands

All deep-water pelagic biota are thought to depend on sinking particles originating from surface waters. Most of the metabolic activity in the ocean is mediated by microbes, particularly in the ocean’s interior. Consequently, the microbial carbon demand—the sum of heterotrophic microbial biomass production and respiration—should roughly match the sinking particle flux. Indeed, in the meso- and oligotrophic North Atlantic, heterotrophic microbial biomass production declines with depth, in line with the sinking particle flux modeled from sediment trap data[52] (Fig. 5). Microbial respiration, however, has been shown to vary less in dark ocean depth profiles than biomass production throughout the Atlantic[18,26], resulting in a much higher microbial carbon demand when compared with the sinking particle flux (Fig. 5). This mismatch between microbial organic carbon supply and demand has been reported for the Atlantic and the Pacific[17,18,53].

Dissolved organic matter represents a large pool of carbon in the deep ocean. However, this dissolved carbon pool is largely refractory[38] and contributes less than 15% to the carbon demand of the heterotrophic microbial community[54]. Buoyant particles, amounting to about 5% of the deep-water dissolved organic carbon concentration, at least in the Atlantic, are collected only inefficiently by sediment traps, and represent an additional source of organic carbon for the dark ocean biota. Layers of these buoyant particles are associated with lower oxygen concentrations[15], indicative of utilization by particle-associated microbes. Their contribution to the organic carbon demand of deep-sea microbes, however, is yet to be determined.

The activity of chemolithoautotrophic bacteria and archaea turns out to be substantially higher than assumed, and represents another potential source of organic carbon in the meso- and bathypelagic ocean[55,56]. Chemolithoautotrophic bacteria and archaea use reduced inorganic compounds as an energy source, and carbon dioxide as a carbon source for biomass production[57]. Based on the availability of energy sources — that is, reduced inorganic compounds — it was assumed that chemolithoautotrophy was ecologically and biogeochemically only relevant in anaerobic layers of sediments, in anoxic water bodies and in oxygen minimum zones[58]. Evidence is accumulating, however, that a variety of reduced inorganic compounds, such as hydrogen, sulphide and ammonia, may be used as an energy source by pelagic microbes in the oxygenated water column of the dark ocean[56,57]. This ability to make use of such a wide range of energy sources indicates that there is substantial niche differentiation in the dark ocean. This niche differentiation probably results from the presence of particles in the seemingly homogenous oceanic water column[59].

Surprisingly, dissolved inorganic carbon fixation in the dark ocean by chemolithoautotrophic bacteria and archaea is of the same order of magnitude as heterotrophic biomass production[55,60] (Fig. 6). As such, it seems that a sizeable amount of new organic matter, in the form of microbial biomass, is synthesized in the dark ocean, potentially fuelling the heterotrophic food web[25,61]. But adding the organic carbon produced by the chemolithoautotrophic microbial community to the amount of sinking organic carbon is not sufficient to sustain the metabolic demands of the heterotrophic community of the dark ocean of the Atlantic[60] (Fig. 5). Hence the mismatch between deep-water microbial energy supply and demand remains to be solved.

Enigmas of the dark ocean

Our understanding of the biological pump has grown significantly in recent years. Phytoplankton community composition has emerged as a key determinant of sinking particle flux, and particles have emerged as hotspots of microbial activity. In addition, buoyant particles and chemolithoautotrophic microbes have emerged as a potentially significant source of carbon to heterotrophic biota in the deep ocean. Despite such advances, however, key challenges remain.

Resolving the remaining discrepancy between deep-ocean energy supply and demand[62] is one such challenge, as is ascertaining how microbes convert labile dissolved organic matter into refractory dissolved organic matter. This process, termed the microbial carbon pump, affects the efficiency of the dark end of the biological pump[63]. It is truly intriguing that about 40 μM of dissolved organic carbon in the dark ocean has an apparent age of about 6,000 years[64]. What makes this dissolved organic carbon resistant to microbial degradation remains unclear. Microcosm experiments indicate that microbial communities have the potential to metabolize some of the recalcitrant dissolved organic carbon in the deep water[65,66]. But it might well be that under *in situ* pressure conditions, microbial activity differs substantially from that commonly measured under surface pressure conditions.

In this respect, we do not even know whether hydrostatic pressure inhibits or stimulates the activity of bulk microbial communities in the dark ocean[67,68]. And the fraction of piezophilic (that is, pressure-loving) or piezotolerant (pressure-tolerant) microbes in the deep ocean is unknown[68]. If the majority of deep-sea microbes are piezosensitive (pressure-sensitive), then we may have overestimated microbial metabolism in the dark ocean. Conversely, if the majority are piezophilic, we may have underestimated their activity. In any case, there is an urgent need for more detailed studies on the effect of hydrostatic pressure on microbial activity in the dark ocean.

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Ocean warming, and associated changes in temperature, oxygen concentration and stratification of the water column, will have an impact on the remineralization depth of sinking particles. Models indicate that even modest changes in remineralization depth could have a substantial impact on atmospheric carbon dioxide concentrations, owing to a redistribution of remineralized carbon among deep water masses[12]. For instance, the shoaling of the remineralization depth that could result from an increase in the temperature and stratification of surface waters could shift carbon towards the surface, and so increase oceanic emissions of carbon dioxide, setting in motion a positive feedback on atmospheric carbon dioxide concentrations[12]. Evaluating the effect of climate change on the efficiency of the biological pump in the dark ocean is challenging because of the latitude-specific changes in water column stratification, phytoplankton community composition and export production expected[69].

Shedding light on the dark end of the biological pump — key to the cycling and sequestration of carbon in the ocean — will require a multidisciplinary approach, particularly in the wake of significant oceanic change.

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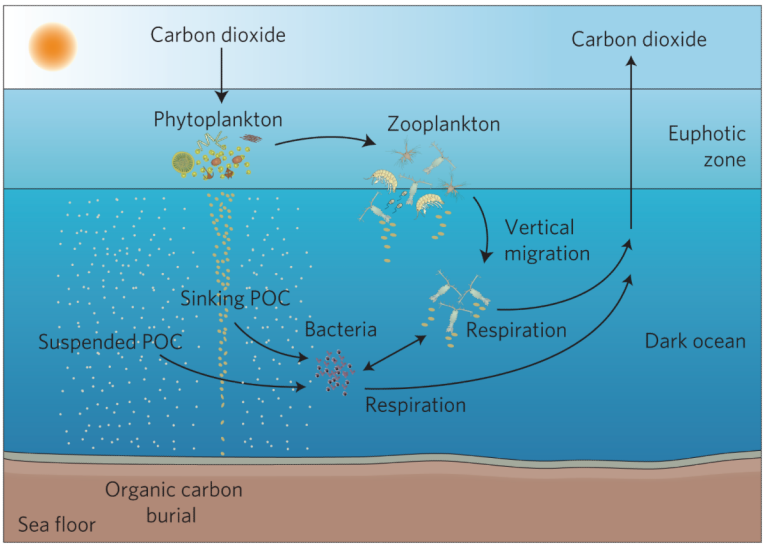

Figure 1. The biological pump

Phytoplankton in the euphotic zone fix carbon dioxide using solar energy. The particulate organic carbon (POC) produced is grazed on by herbivorous zooplankton, or consumed directly or indirectly by heterotrophic microbes feeding on solubilized remains of phytoplankton. Between 1 and 40% of the primary production is exported out of the euphotic zone, and it exponentially attenuates towards the base of the mesopelagic zone at around 1,000 m depth. Remineralization of organic matter in the oceanic water column converts the organic carbon back to carbon dioxide. Only about 1% of the surface production reaches the sea floor.

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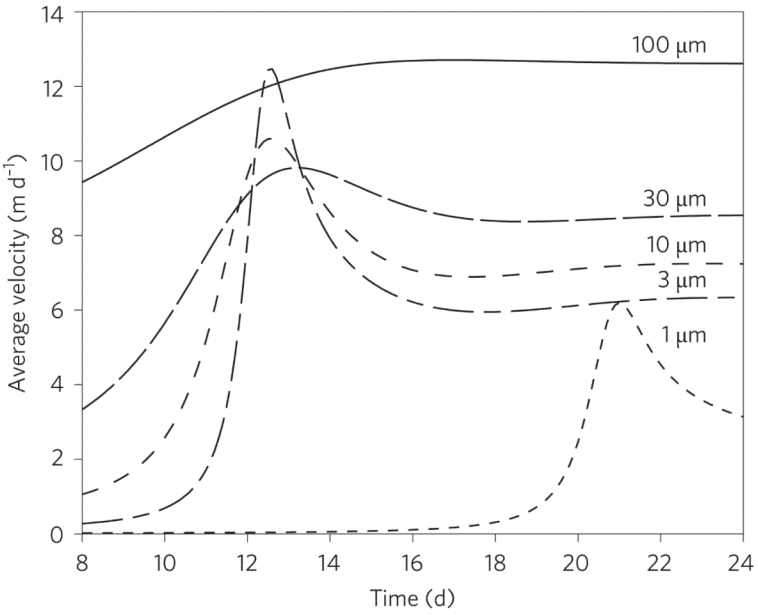

Figure 2. Sinking velocity of different phytoplankton size classes

Average sinking velocity versus time (in days) for phytoplankton cells with initial diameters of 1, 3, 10, 30 and 100 μm. Algal cells are considered to collide, forming aggregates at rates that depend on their abundance and size. Large cells settle faster than small ones. With time, cell concentrations increase, causing an increase in the fraction of material in aggregates. The resulting increase in average particle size leads to an increase in average settling speed with time. Peaks in total cell concentration occur when enhanced losses due to settling balance gains due to cell division. The maximum average settling rate of particles formed from 1 μm cells is not substantially different from that of particles formed from 30 μm cells. Reproduced with permission from ref. 16, © 2007 AAAS.

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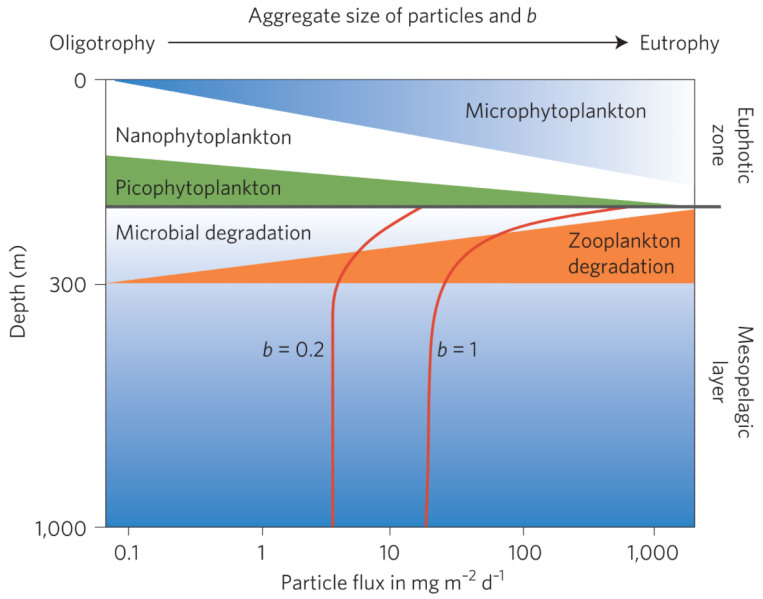

Figure 3. Processes affecting the flux of particles in the ocean

The widths of the coloured surfaces in the euphotic zone represent the relative contribution of different phytoplankton size classes to particle export under nutrient-poor and nutrient-rich conditions. The aggregate size and the slope *b* increase from oligotrophic to eutrophic systems. This transition is due to an overall community shift from picoplankton (size range 0.2-2 μm) to nanoplankton (2-20 μm) and microplankton (20-200 μm). Below the euphotic zone, microbial or zooplankton degradation alters the initial particulate organic carbon flux indicated by the curve (red lines) using the typical slope values (*b*) found for oligotrophic (*b* = 0.2) or eutrophic (*b* = 1) ocean regions. Modified with permission from ref. 17, © 2009 Association for the Sciences of Limnology and Oceanography.

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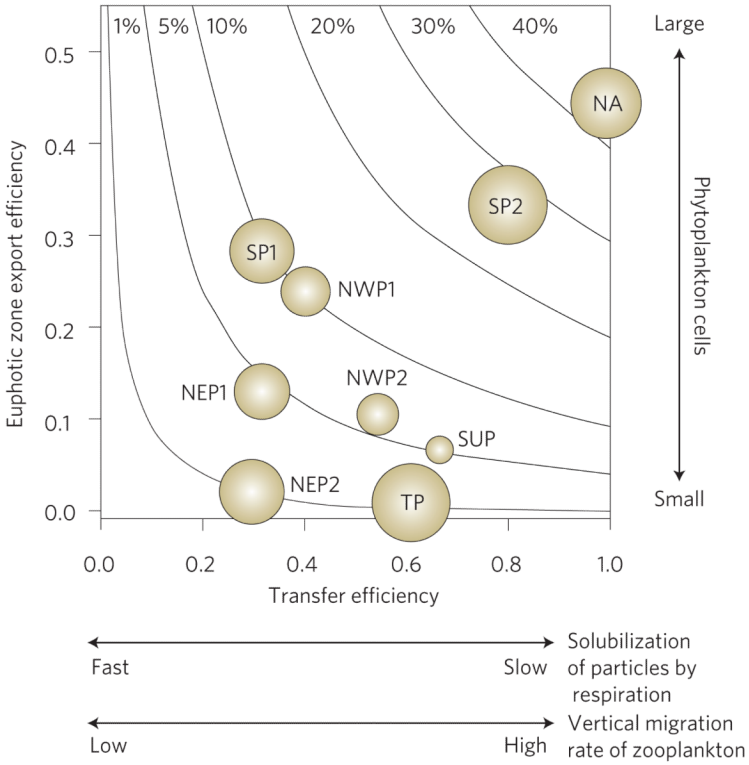

Figure 4. Model relating the export efficiency to the transfer efficiency of the biological pump

Low export efficiencies indicate that most of the attenuation of net primary production is already taking place in the euphotic zone. Low transfer efficiencies suggest rapid reduction of particulate organic material between the base of the euphotic zone and 100 m below. The circle sizes are proportional to the magnitude of net primary production. The contour lines from 1 to 40% represent the flux of export production as a function of euphotic zone export and transfer efficiency. Arrows of parameters along the *y* and *x* axes indicate some processes that would move a particular oceanic site higher or lower on these scales. NA, North Atlantic; SP, South Pacific; NWP, northwest Pacific; NEP, northeast Pacific; SUP, subtropical Pacific; TP, tropical Pacific. The numbers attached to the region names indicate different sites or seasons. Modified with permission from ref. 13, © 2009 Association for the Sciences of Limnology and Oceanography.

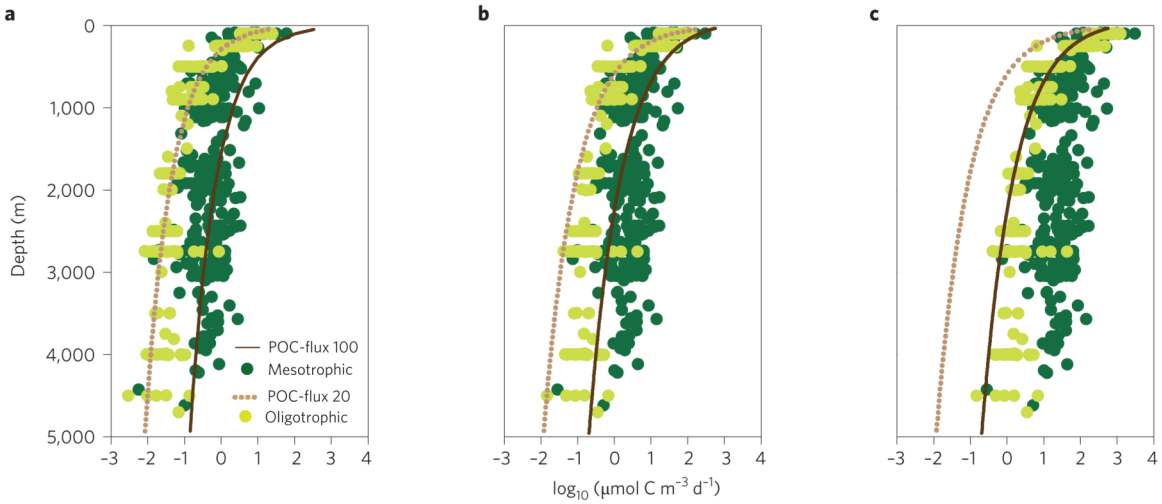

Figure 5. Microbial carbon demand and particulate carbon flux in the mesotrophic and oligotrophic North Atlantic

a, Depth-dependent microbial biomass production, as measured by carbon uptake. **b**, Microbial carbon demand based on measured biomass production and applying an average open-ocean microbial growth efficiency of 20%. **c**, Microbial carbon demand based on measured biomass production and a measured microbial growth efficiency for the dark ocean of 2% according to ref. 60. Also shown is the depth-dependent particle flux calculated from a model (from ref. 52) using primary production values reflecting the mesotrophic and oligotrophic North Atlantic. In **b** and **c**, dissolved inorganic carbon fixation by microbes is added to the output of the flux model assuming that chemolithoautrophy represents a fresh source of non-sinking organic carbon in the dark ocean. Data from T. Reinthaler *et al.*, unpublished.

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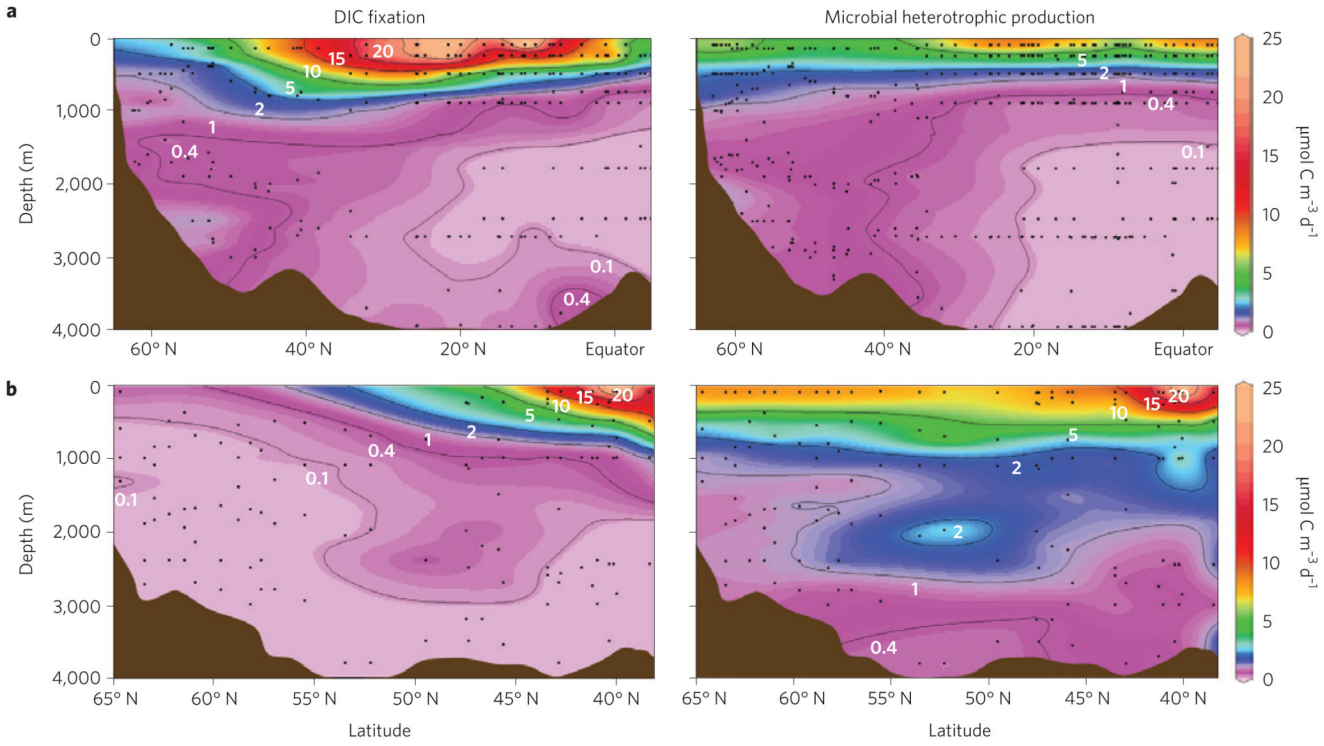

Figure 6. Microbial inorganic carbon fixation and microbial heterotrophic production in the North Atlantic

a,**b**, Dissolved inorganic carbon (DIC) fixation and heterotrophic production in the eastern (**a**) and western (**b**) North Atlantic basin. Black dots indicate the latitudes and depths where samples were collected. Black contour lines and related numbers indicate rates (μmol C m^{-3} d^{-1}). Reproduced with permission from ref. 60, © 2010 Elsevier.

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